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CONTRIBUTION TO OUR KNOWLEDGE OF THE MYXINOIDS.¹

JULIA WORTHINGTON.

INTRODUCTION.

EVER since Johannes Müller introduced the Myxinoids to the scientific world, interest in these primitive forms has continued unabated, both as regards their peculiarities of structure and function and their consequent position in the vertebrate series, and the interrelations of the different varieties among themselves. Owing to the wide geographical distribution of the Myxinoids, the relative scarcity of individuals, and the difficulty of securing material for study, especially the living animals, previous papers have been based upon the study of museum specimens, and our knowledge has, in consequence, been very incomplete. It was my good fortune to obtain, during the summer of 1904, several hundred individuals of *Bdellostoma dombeyi* Lac. in sound, healthy condition, which I kept alive in aquaria. I was able to provide conditions closely approximating their usual habitat, and, under these favorable circumstances, I kept them under constant observation for four months. The observations made have been checked by a study of the conditions of their normal habitat. This paper, therefore, is based mainly upon a study of living individuals in conditions approaching as nearly as possible the normal environment; and these notes are published in the hope of throwing some new light upon this interesting form, and for the purpose of correcting some erroneous statements that, through lack of means of observation, have gained currency.

I wish to express my thanks to Dr. C. H. Gilbert, of Stanford University, who kindly placed at my disposal the facilities of Stanford's seaside laboratory at Pacific Grove, California; to

¹ Under the direction of Dr. Howard Ayers.

Dr. Frank McFarland for helpful suggestions ; and to Mr. M. H. Spaulding for much practical help. I wish also to thank Dr. Michael Guyer, of the University of Cincinnati, for the loan of laboratory materials, and to express my obligations to my sister Louise for the very excellent and accurate drawings from which the illustrations for Fig. 1 and 2 were made.

The Myxinoid upon which the following observations were made, is the common hagfish of the Pacific coast, *Bdellostoma dombeyi* Lac. It is found in exceeding abundance in the Bay of Monterey, where it is a great pest to the fishermen. It is caught both with hook and line, and in traps. Those caught on hooks do not live long in captivity. Instead of being hooked in the jaw as is usual with other fish, *Bdellostoma* usually swallows the baited hook whole, and is thus hooked through the head or the body wall, hence the esophagus and stomach are more or less torn in extracting the hook. Even under most favorable conditions I have not found those caught on hooks to live more than a few hours in aquaria. The traps used by the fishermen in catching hagfish, are large wicker baskets, loosely woven, resembling lobster pots. A quantity of bait, usually pieces of squid or sardines, is put inside, and the trap sunk over night. In the morning it may contain anywhere from twenty-five to a hundred fish, mostly medium size, with a few small and several large individuals. The largest hagfish are not caught in the traps, as the meshes of the baskets used are too small for them to pass through.

The aquarium, in which I kept them, was a wooden tank, about six feet long, four feet wide, and two feet deep. It was located in the basement of the laboratory, a large, cool room, well lighted. The water in the tank was kept about a foot deep, the bottom was covered with a thin layer of clean sand, and stones were loosely piled in one corner to furnish hiding places. Four streams of fresh salt-water, coming from glass pipettes, with a length of stream varying from two to four feet between the glass and the surface of the water, played constantly into the tank, supplying fresh, well aerated water. Here the colony lived throughout the summer. Although some two hundred and fifty fish were thus kept under observation,

not more than six or eight of the total number died a natural death. Of these two hundred and fifty, about seventy-five were kept in the aquarium from six weeks to two months or more before I killed them, and more than a hundred were kept for a month before being killed.

GENERAL DESCRIPTION.

It is not necessary to describe the general appearance or characteristics of *Bdellostoma*, as that has already been admirably done (Ayers, '94); but one or two points of interest were ascertained in reference to their size. Of 550 specimens measured, the longest was 24.5 inches, while 104 measured 20 inches or over, and 64 were between 19 and 20 inches long. When it is remembered that of these 550 specimens, between 350 and 400 were caught in traps that did not favor the ingress of the larger hagfish, the average length will be seen to fall in the neighborhood of 19 to 20 inches. In regard to their length at hatching, the smallest free-swimming hagfish that fell into my hands measured scant two and three eighths inches (60 mm.), while a few days later I took an embryo from the shell that measured a trifle more than two inches and a half (65 mm.). This embryo was apparently ready to hatch, as it swam vigorously as soon as it was freed from the shell.

These newly hatched hagfish have the same shape as the adult, the only perceptible difference between them and their elders being that their tentacles are relatively a little longer than those of the mature fish. At the time of hatching, the head is an eighth of an inch in diameter; when from twelve to fourteen inches long the proportions of head to body are somewhat different, the head measuring from three eighths to one half inch across, and thus being relatively thinner. When about fifteen inches long, however, the hagfish begin to increase rapidly in girth, measuring at least three fourths of an inch across the head, while the larger ones measure still more. This marked change of form does not, however, as might be thought, mark the time of sexual maturity, for an individual only twelve inches long and slim in proportion was found to have a well

developed ovary, with eggs in the process of yolk development. In regard to the age at which these changes take place, we have as yet no definite information. As is already known, the process of development within the egg is slow, when compared with the rate of growth of other vertebrate embryos; and their post-embryonic growth is probably also very slow, for very small fish (*viz.*, thirteen or fourteen inches long) kept in the aquarium for three months, showed at the end of that time no perceptible change in form or size, although they fed in a normal way, or at least, as normally as any other fish in the aquarium.

One of the most interesting points about *Bdellostoma*, because of its supposed taxonomic value, is the variation in the number of gills. Taking the number found in the hagfish of different geographic regions as a basis, the *Bdellostomids* have been divided not only into different species, but also into different genera, *Bdellostoma forsteri*, of the Cape of Good Hope, with its six to seven gills on each side being placed in one genus, and the *Bdellostomas* of the American Pacific coast in another, subdivided into two species, *Bdellostoma dombeyi*, with ten gill slits, found in Chilean waters, and *Bdellostoma stouti*, whose usual number of gill slits is eleven or twelve, in the waters of California. Dr. Ayers ('94), after a careful comparison of the Cape of Good Hope and California varieties, concluded that there was no specific, far less generic difference between the two forms, and stated that they, together with the Chilean variety, belonged to one species, the preferable name for which was *Bdellostoma dombeyi*. This conclusion was scouted by Howes ('94), but purely on *a priori* grounds, and without any study of the forms in question. Since this time not much work has been done that would throw light on this question until within the last year or two, when Dean, studying the hagfish found off the coast of Japan, came across a variety that he called *Homea okinoseana*, distinguished by having eight gills on each side, but in all other respects like the hagfish of other localities. This Japanese variety thus fills in the gap between the Cape form with its six to seven gills, and that of Chile, with ten gills on each side.

It is worth while to study the California form carefully and in detail with regard to the gills. Dr. C. H. Gilbert of Stanford

University, quoted by Jordan and Evermann states that in fifty-four specimens which he counted, forty-one had twelve gills on each side, twelve had eleven gills, and one had thirteen gills. He states also that he occasionally found one with ten or fourteen on each side, but that the normal number was twelve. Worked out in percentages, this would read :—

Individuals with 12 gills	75.9 %.
“ “ 11 “	22.2 %.
“ “ 13 “	1.8 %.

When tested by the examination of larger numbers of individuals, however, these figures undergo considerable modification, and a new factor enters in, *i. e.*, fish that have a different number of gill slits on the two sides. The following table is given by Dr. Ayers in his paper published in 1894 :—

101	individuals	had	11	gill	slits	on	both	sides ;
26	“	“	11	“	“	“	one	side and
			12	“	“	“	the	other ;
208	“	“	12	“	“	“	both	sides ;
11	“	“	12	“	“	“	one	side and
			13	“	“	“	the	other ;
8	“	“	13	“	“	“	both	sides.
<hr/>								
354	total number of individuals counted.							

Worked out in percentages this reads :—

Individuals with 11 slits on each side	.	.	.	28.5 %
“ “ 11 “ “ one “ and	.	.	.	
“ “ 12 “ “ the other	.	.	.	7.3 %
“ “ 12 “ “ each side	.	.	.	58.7 %
“ “ 12 “ “ one “ and	.	.	.	
“ “ 13 “ “ the other	.	.	.	3.1 %
“ “ 13 “ “ each side	.	.	.	2.2 %

These figures, as will be seen, reduce the percentage of those having twelve slits on each side by one third, add very nearly one third to the percent of those with eleven slits on each side, increase slightly the percentage of those with thirteen on each side, and introduce the two intermediate forms, those with

eleven and twelve slits, and those with twelve and thirteen, these two together amounting to 10% of the total number. Dr. Ayers also says: "Of the eight 11-12 variation, where the position of the gills was noted, four had eleven gills on the right side, and twelve on the left, while the other four were just the reverse, with twelve gills on the right side and eleven on the left." On looking over the count of five hundred and fifty hagfish that I made while at Pacific Grove, I find still greater variability in the percents.

No. of Individuals	No. of Gills		Percent
	Left	Right	
1	10	11	.18
3	11	10	.54
123	11	11	22.36
25	11	12	4.54
44	12	11	8.
325	12	12	59.09
7	12	13	1.27
15	13	12	2.72
7	13	13	1.27
<hr/> 550			

This larger count gives practically the same percentage of individuals with twelve gills on each side as do Dr. Ayers's figures, reduces that of those with eleven gills on each side about one fourth, increases the sum of the 11-12, and 12-13 variations from 10.4% to 16.5%, diminishes those having thirteen gills on each side from 2.2% to 1.27%, and introduces a new variation, 10-11 gills, this kind being .72% of the total number. This last variation makes direct connection with the Chilean variety with ten gills on either side. It will be noticed in my figures that in the three uneven variations, 10-11, 11-12, 12-13, the total number of individuals having the larger number of gills on the left side is sixty-two against thirty-three, almost two to one. This point will be discussed a little later.

The table following combines the records of Dr. Gilbert and Dr. Ayers with my own.

No. of Individuals	No. of Gills	Percent
4	10-11	.41
236	11	24.63
95	11-12	9.92
574	12	59.92
33	12-13	3.44
16	13	1.67
<hr/> 958		

A total of 958 individuals certainly gives a reasonably safe number on which to base conclusions. In this table as in the others, the fact stands out prominently that in the California hagfish twelve gills on each side is the number most commonly found. But when the number having it only amounts to 59.92% in a total of 958 eels, it cannot well be called the normal, or even the usual number, and consequently I agree with Dr. Ayers that the usual number of gill slits is eleven or twelve.

That 13.7% in a total of 958 eels is found where the number of gills is greater on one side than on the other, is to me one of the most significant features in the proper specific classification of the *Bdellostomids*. With six and seven gills the prevailing number in *Bdellostoma forsteri*, eight in that found in Japan, ten the number in the Chilean form, and eleven and twelve in California, varying on the one hand, though rarely, to ten, and on the other hand more frequently to thirteen, it is surely no longer possible to divide these animals into different genera and species on the basis of the number of gills alone; the count of teeth (Ayers, '94), is equally unsatisfactory as a ground for division into species, and no other ground for such division has ever been advanced.

As a matter of fact, the differing number of gills in the California hagfish is even more significant when the animal is examined more closely, externally and internally, than when the external apertures alone are counted. On dissecting the gill region of those animals with an unequal number of gills on the two sides, we find not merely that the number is variable, but also where the variation is most apt to occur. Referring back to my table, and noting the fish with an unequal number of gills

on the two sides, we find that the fish in which the greater number of gills lies on the left side (the side of the ductus œsophagocutaneus), occur about twice as often as those in which the greater number is on the right side. But when the thoracic cavity of these particular fish was dissected, I found several cases where the number of external openings and the number of gills did not correspond.¹ Of the sixty-two individuals, in which the left gill slits outnumbered the right, six had the last gill on the left side, that which should open into the ductus, entirely wanting, making an even number of gills on each side. Two of these six were in the 11-12 group, four in the 12-13 group. In regard to the position of the external openings only one was at the normal distance from the ductus, in two the distance between ductus and external aperture was one half the normal distance between these openings, in two the external aperture lay very close to the edge of the ductus, and in one it lay in the cephalic edge of the ductus.

In other fish in which the number of gills on each side was uneven, where the greater number was on the left side, five had the last gill, that which opens into the ductus, rudimentary, varying from one fifth to one half the size of the normal gill, and in one of these the opening of the ductus was one half the usual distance from the external aperture nearest it.

In all of the fish examined by me that had the greater number of gills on the right side, the gills were normal, and normally placed. But another curious variant was found in the 12-11 series that has a marked bearing on the question, whether the change in the number of gills in the different varieties is due to addition or suppression. This individual had twelve gills on the left and eleven on the right side. The twelfth gill was of normal size and at a normal distance from its neighbor, but the second gill on the left side (counting from before backwards), was missing, the external opening leading into a short *cul de sac*. The first gill on the same side was rudimentary. If there were

¹ It should be stated here, that in counting gill slits, *i. e.*, the external apertures, the external opening of the ductus œsophagocutaneus is always counted as one, as the external aperture of the last gill on that side usually lies not on the outer surface, but in the ductus just inside the opening.

either a fixed or a normal number of gills, this could only mean that this particular animal was a freak. But where we have variations of the species in which the number of gills ranges from thirteen to seven, and one variation (that from California), in which no number can be considered either normal or fixed, and where the last gill on one side is found to be either rudimentary or missing, there is certainly an indication of a tendency to the suppression of the gills. Moreover, in the last case the rudimentary and the missing gill are both in an unusual place (the cephalic instead of the caudal end of the line). Still another variant bears out this view. This variant was one of the even-numbered group, with twelve gills on each side. On opening the thoracic cavity, it was found that while the fish had twelve normal gills on the right side, on the left the first was missing, and the second rudimentary. As in the case last mentioned, the external aperture of the missing gill led into a *cul de sac* and there was no pharyngeal opening. In this fish there was no external mark to indicate the slightest abnormality within, which raises the question: What percentage of abnormality would be found if careful dissection were made of the gill regions of a large number of individuals?

There is no particular size in which these variations occur. In the last one given, the fish was only eleven and one half inches long; in the one preceding, twenty-one and one half inches long; the others varied between these two. It would be interesting if some young hagfish with an uneven number of gills, particularly individuals where the distance between the ductus and the nearest gill is less than normal, could be kept under observation for a number of years, to see if any changes occur during the life of the individual, or if these variations are fixed during larval growth and remain fixed during adult life. It would also be of great value in this connection if the other varieties of hagfish could be more carefully studied, to determine if the variation in the number of gills is as great as that of the California hag, and if so, when the variations occur. It should also be determined whether the number is more constant among the groups having a small number of gills.

HABITS AND HABITAT.

The hagfish abounds in the Bay of Monterey, and is taken on the regular fishing grounds, particularly on the rock-cod beds, at a depth of about three hundred feet. The bottom here is rocky and coated with a thin, smooth sediment, but without any great amount of sand or seaweed. Infrequently it is captured in shallower waters along shore where the bottom is sandy. From observation of several hundred individuals, I find that in the aquarium they evidently prefer the hard bottom when at rest, lying for the most part coiled in and out among the rocks, sometimes with their heads under cover, but more often with about two inches of the head projecting freely into the water. When not among the rocks, or not swimming, they rest coiled up on the bottom of the tank (Fig. 2), occasionally resting on the sand, but more often on the wood where the sand has been pushed aside. At a time when there were about thirty fish in the tank, I kept watch for a week to see how many chose the different kinds of bottom. I transcribe here the notes taken at the time.

July 24, A. M. All were among the rocks but two. Of these two, one was curled entirely on the wood, the other curled on the wood with its head resting on the sand.

July 24, P. M. Two were lying entirely on the wood, the rest were among the rocks.

July 25, Noon. The same as on the previous day. After pouring water on them vigorously, and so stirring them up to swim around, six settled finally on the wood, two of them with their heads resting on the sand, while the others returned to the rocks.

July 26, Noon. Two were on the wood, the rest among the rocks.

July 26, P. M. All were among the rocks.

July 27, A. M. Two were on the wood, the rest among the rocks.

July 28, Noon. One on the wood, the rest among the rocks.

July 29. Two on wood, one on sand, the rest among the rocks.



FIG. 1.—Hagfish coiled among the rocks. $\times \frac{1}{2}$.

July 30, A. M. Three on wood, one of them with its head touching the sand, the rest among the rocks.

July 30, P. M. Five on wood, the rest among the rocks.

Aug. 1, A. M. All among the rocks.

Aug. 1, Noon. Five on the wood, two of them partly touching sand, the rest among the rocks.

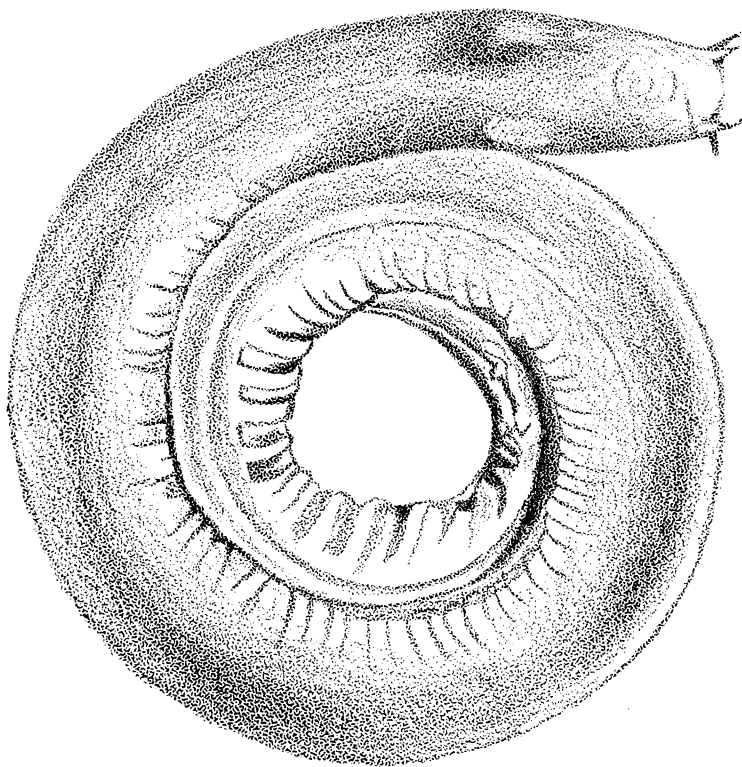


FIG. 2.—Hagfish at rest on the bottom of the aquarium. Natural size.

At a later date when there were one hundred and thirty fish in the tank, two more observations were made. The first showed only sixteen of the hundred and thirty fish on the sand, the second only fifteen. A few days later with one hundred and twenty-four fish in the tank, only twelve were on the sand.

Unquestionably then, in the ordinary circumstances of life, the hagfish prefers a hard bottom to rest on. If the rock heap

is overcrowded, and the bare wood spaces preëmpted, those left out will, for the most part, gather together and form a tangled coil, looking much like the conventional Medusa's head.

Perhaps another factor entered into this consideration of bottom, however. Was it altogether a feeling of touch that governed their choice of resting place, or did color play a part? Did they prefer the dark to the light? Two hagfish were transferred to an ordinary aquarium with glass sides and a zinc bottom. Half of this bottom was covered with sand to the same thickness as that in the large tank, and the sand and zinc were nearly the same color. The fish were kept here for several weeks, and acted just as they had in the large wooden tank. They coiled persistently on the hard zinc bottom, against the side of the aquarium, or against the iron waste pipe, seldom being found on the sand. After a few days I put a rock in the midst of the sand bottom, and after that one or the other would be found lying against it, but otherwise they shunned the sand, showing that it was purely a sense of touch that guided them.

The hagfish seem to have great power of resistance to unnatural environment, judging by the way they are handled by the Monterey fishermen, and the condition in which they reach the laboratory. They are taken from the traps between six and ten o'clock in the morning, dumped, fifty of them together, into an oblong can with a base about ten inches square and sides perhaps eighteen inches high, barely covered with water, and then stowed somewhere in the bottom of the boat while the fisherman finishes his business and rows to shore, a distance of two or three miles. Arrived on shore, they remain sometimes for several hours in the same uncovered cans before transportation to the laboratory. At the laboratory they undergo one more handling, as they are counted on being put into the aquarium. But in spite of this long wait in very little, poorly aerated water, but few die, though they are greatly crowded, and sometimes roughly handled. The long exposure to the air likewise seems not to affect them if the weather be not too warm, and the can not too full, so that the sun does not strike directly upon them. Of the first catch of about fifty, all lived; and of the second of one hundred and thirty-two, brought up in two

cans, thirty or forty were sick on arrival, but the next morning two only were dead, and all the rest in fine condition. It is noticeable that the young ones have, as a whole, more power of resistance than the old ones, for they would arrive fresh, as though just from the depths of the bay, no matter how sick many of the older ones were.

There is one unfailing test of the general condition of the hagfish: its geotropic reaction. When well and at rest, it is invariably coiled up more or less tightly, either in a spiral by itself (Fig. 2) or in and out among the rocks. Even if the fore part of its body lies free and sinuous, the tail is coiled. But if exhausted or sick, the coil straightens out, and it lies in a crescent form. The sicker it is, the straighter it becomes, and when dead it lies entirely straight.

The hagfish can live out of water without injury for a great many hours if kept in a cool, damp place. I often found on visiting the tank in the morning, that one or more of the smaller fish had found the water outlet while swimming in the night, and had slipped to the floor. They would be tightly coiled on the cool, moist cement floor, and were as agile and active there as in their native element.

There is one condition, however, that the fish cannot endure: a rise in temperature. The water on the surface of the Bay of Monterey averages in summer 64° F. or 17.7° C. What it is at a depth of two hundred feet, I do not know, nor how cold it gets in winter. But the air at Monterey is never so cold as to kill palms or heliotrope, so the water cannot become very cold. The water in the tank in which I kept the fish averaged 22° C., and in that they thrive. On a warm sunny morning, I placed two young hagfish in a tank about three feet long by one foot wide, covered them with about five inches of fresh salt water at 22° C., and placed the tank by a window, where the sun shone directly into half of it, leaving the other half of it shaded. Under the heat of the sun the water in the tank rose gradually to 30° C. As the water became warmer, the fish grew very restless and languid, swimming constantly, not rapidly as usual, but with a slow, jerky movement as though seeking to escape the warm water. At the end of two hours and a half one of

them was lying almost straight. Both were put into the small aquarium with running water at a temperature of 22° C.; they swam freely for a few minutes, then settled down against the outflow pipe, having regained their normal habit. This was between half-past twelve and one o'clock. It was an exceedingly warm day, the thermometer standing at 89° F. in the shade, and the aquarium was so placed that the afternoon sun streamed directly upon it. About five o'clock I noticed that the two hagfish were very languid and stretched almost straight. On testing the water I found that it had risen to 29° C. Suddenly, the hagfish, without anything being done to disturb them, began to swim in a very violent, jerky way, and to throw out strings of slime, which is never done except when they are irritated. They would swim and stop intermittently, always lying at full length when at rest, and swimming so irregularly and violently as to injure themselves. When put into cooler water, 22° C., they immediately settled down quietly, half stretched out. I placed them in a small wooden tank in the cellar, by the large tank, in order to keep them separate from the other fish for a while, and note what after-effects there might be. The next morning one of them had escaped to the floor, together with two from the large tank. Of these three, two were entirely normal, and one was dead, in all probability the one that had been exposed to the heat the day before. The other hagfish grew steadily more languid, and died at noon the next day, two days after the experiment. Both fish were in a normal condition when the experiment began. It was positively the heat from which they suffered, and not the actinic rays, because they had been exposed to brilliant sunshine every afternoon for a month, and no ill effects had followed. The day they were affected was the first day there had been a marked rise in temperature.

Taken as a whole the hagfish do not lead an active life. When thoroughly aroused and on the alert, they swim at a very high speed, with a graceful, serpentine motion, but for the most part, they lie placid, perhaps motionless, perhaps lazily moving their heads from side to side. They are more active by night than by day. In the daytime more than once I found some of

them asleep. There was no outward difference between the sleeping ones and the others; all were curled quietly on the bottom, but if by chance a sleeping one was touched, instead of wriggling away it remained passive, unless perchance it coiled tighter, retaining its coil even when lifted from the water. Once I found two sound asleep, surrounded by a mass of slime in which they had in some way become lodged. The slime served them as a buoy, and they were floating quietly in it on the surface of the tank, circling around with the current. I took them out and stripped their covering from them, but they hardly aroused while I did so, and settled down to sleep again as soon as they were put back into the tank. Sometimes after a minute or two of handling they awake, but an interval elapses between their first stirring when they squirm uneasily in the hand, and full alertness when they swim rapidly away, or if held tight, they make the usual vigorous efforts to free themselves. If before the fish is wide awake, it is put back gently, it can drop off to sleep again. I once lifted a sleeping fish, dropped it into a pail, carried it a distance of more than two hundred feet, took it out of the pail, and started to decapitate it. All this motion followed by the tight grasp of my hand and the first touch of the shears, usually the first signal for the most frantic struggles, did not rouse it perceptibly, and its head was off before it began to squirm.

It is interesting to watch their movements, while they are becoming accustomed to confinement. When the first lot of fifty were placed in the tank it contained only water. They were normal fish in every respect and when first placed in their new home they swam around very vigorously, threw out a great deal of slime when touched, and were on the whole, unusually excited. After a short while, they settled down on the bottom, in the usual coils (Fig. 2), an occasional group of three or four together, the rest separate. Two days later sand was put on the bottom, and the rock pile built at one side. In a few hours all had burrowed among the rocks. There they lived very quietly, seldom moving when left to themselves, except at night. For the first four or five days they were easily aroused by dipping a small pailful of water from the tank and pouring it on

them. When this was done they would throw out great quantities of slime, and wriggle among the rocks, some of them leaving the nest, and swimming rapidly around the tank. When the sixth day came it was harder to rouse them, and for about ten days following they could hardly be stirred, neither throwing out slime nor swimming when the water was troubled. If one was lifted on a stick and moved, it quickly settled down wherever it might be, finding its way back to the rocks later. This was not due to illness, for their positions were normal. Toward the latter part of the third week, they became more active, lying quietly in the rocks when undisturbed, but rousing easily and getting much excited when water was poured on them from a pail, swimming freely and throwing off slime again, as they had done at first.

The second lot I received went through the same stages of liveliness and torpor as the first, and in about the same time intervals.

The so called slime they throw off is their chief means of protection. It often enables them to escape from whatever would catch them, by forming a covering so slippery that it is difficult if not impossible to get or keep hold of them. The thread cells are not emitted except upon sufficient provocation. I have often lifted them carefully and had them slip through my fingers without causing thread cells to escape. It is their response to conditions that irritate; they are always thickly surrounded with slime when caught on the hook, and the occasional ones that died natural deaths in the tank had always thrown off a considerable amount of slime in dying.

The question of what and how the hagfish eat, is one that has been much discussed in previous papers about them, some writers maintaining that they are parasites, and all stating that they are extremely voracious. In regard to this latter point the evidence comes from the fishing grounds. When the night lines are examined, one third or more of the hooks hold hagfish and the fish on many of the others have been entirely eaten away, nothing but the skin and bones being left. The hagfish has bored inside the skin and eaten all the soft parts, and is sometimes caught in the very act of wriggling away at the close of

its meal when the fish is taken from the water. From what I saw of their behavior in the tank, though, I conclude that this behavior shows the inordinate numbers of the fish in the bay, rather than extreme voracity. Those that I had were small feeders, and went a long time without eating. As a matter of fact, they ate so infrequently that I was not able to experiment with them and test their likes and dislikes as much as I wished.

According to the fishermen, the best bait is squid; failing that, they use herring, or as they call them, "sardines."

My first lot was caught on a Friday. The following Monday I put into the tank eight dead flounders about ten inches long and three inches wide. About a dozen of the fifty hags ate freely, some of them ravenously. But although several of the flounders had been partly eaten, the total consumed did not amount to more than two flounders.

It is very interesting to see them eat. The process may be easily watched when they are fed with small fish, or are just beginning on a large one. The feeding apparatus, described by Ayers and Jackson (:00), consists of a heart-shaped plate composed of symmetrical halves that open out and fold together like the leaves of a book. This plate bears on the dorsal surface of each half a double row of horn teeth, their points directed meso-caudad, and it lies imbedded in the membrane of the ventral wall of the pharynx.

When the animal feeds, the tooth plate, which is really a modified and movable lower jaw, and in no sense a tongue, as stated by Müller ('34) and P. Fürbringer, is thrust out of the mouth, and its fore end is drawn down so that it takes a position almost perpendicular to the long axis of the body. The two halves are at the same time drawn apart, so as to present an almost flat surface. Placing this flat surface against the fish to be eaten, the hag draws the halves of the tooth plate together, thus tearing off a portion of the food, and then withdraws it into its mouth. It swallows the food very rapidly, and immediately sticks out the tooth plate for more. There is no sucking motion as Fürbringer has said; the hagfish simply rests with its nose against the fish, and if, because of a current in the water, or through the vigor of the attack, the food is moved from its

position, the hagfish swims rapidly after, keeping in this way in constant touch with it.

This tooth plate is worked by five muscles, three of which form a unique mechanism called by Dr. Ayers the "club." These muscles lie close to the ventral surface and may all be seen when the ventral skin and body musculature are deflected back. The two that do not belong to the "club," lie ventro-cephalad of it (Fig. 3). The more lateral one arises as a narrow

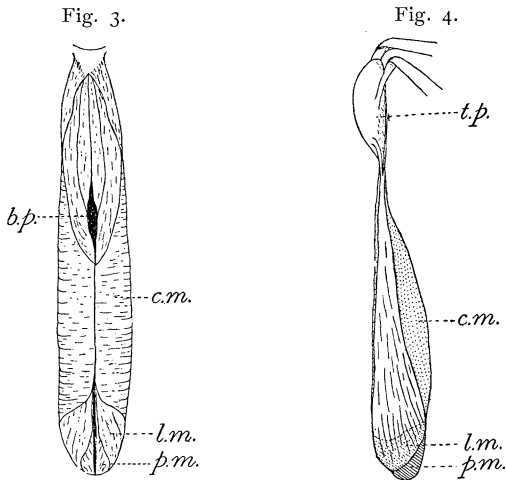


FIG. 3.—The "club muscle" and its accessories. Ventral view. *b. p.*, basal plate; *c. m.*, circular muscle; *l. m.*, long muscle; *p. m.*, perpendicular muscle. $\frac{1}{2}$ natural size.

FIG. 4.—The "club muscle" and its accessories. Lateral view. Half of the circular muscle has been cut away in order to show the long muscle. *c. m.*, circular muscle; *l. m.*, long muscle; *p. m.*, perpendicular muscle; *t. p.*, tooth plate. $\frac{1}{2}$ natural size.

band of fibers along the lateral edge of the cephalic half of the caudal section of the basal plate, runs cephalad, then curves slightly mesad, joining its fellow of the opposite side in a common aponeurosis, about a quarter of an inch behind the mouth opening. The aponeurosis continues forward until it reaches the mouth opening, where it fuses with the connective tissue which supports the mucous membrane of the lower lip; here it divides, each half deflecting posteriorly and laterally, to attach itself near the cephalic border of the tooth plate. The contraction of this muscle helps the two halves of the tooth plate to close together.

This mandibular muscle (Figs. 3, 4), is called by Fürbringer, *m. copulo-glossus superficialis*, and by Müller, "der oberflächlicher Vorzieher der Zunge." Both of these names are now inadmissible, as we are dealing with the lower jaw and not with the tongue as these authors thought.

Mesad of this superficially placed mandibular muscle lies Fürbringer's *m. copulo-glossus profundis*, Müller's "tiefer Vorzieher der Zunge." This muscle (Figs. 3, 4), consists of a lateral and a mesial division which join together at the cephalic end. The lateral division arises from the lateral edge of the caudal end of the third section of the basal plate. Its fibers run laterally, then curving, run cephalad along the border of the mandibular muscle last mentioned. The mesial division also arises from the lateral edge of the third section of the basal plate, between the points of origin of the lateral division of this muscle and the superficial mandibular muscle. It runs forward between the lateral division and its fellow of the opposite side, being separated from the latter merely at its hind end. The combined mesial and lateral divisions of each side fuse together at the cephalic end into a common tendon for the two muscles. This tendon runs cephalad between the basal plate and the aponeurosis of the superficial muscle, turns dorsad at the cephalic end of the latter, and runs caudad to the tooth plate where it divides again and is inserted midway in the length of the latter, close to the median line. This muscle, by contraction, draws the tooth plate forward, and by contracting to its full extent pulls it out of the mouth and into the vertical position.

The other three muscles that manipulate the tooth plate form a structure aptly named by Dr. Ayers the "club muscle." This "club" is between three and four inches long and consists of a hollow circular muscle, a long muscle, and a perpendicular muscle.

Of these three, the long muscle (Fürbringer's *m. longitudinalis linguæ*, Müller's "innere Längsmuskel der Zunge") is the only one in direct connection with the tooth plate. This long muscle (Figs. 3, 4, *l. m.*), is about three inches long, and from half to three quarters of an inch across its caudal end, tapering at its cephalic end to two tendons, one of which lies enclosed within

the other. These two tendons run cephalad to the tooth plate, just before reaching which they separate, the outer tendon attaching itself to the ventral surface of the tooth plate along the median line, the inner one dividing into two which curve laterad, run ventrad of the plate, and insert near the lateral border. The fibers of the long muscle are directed longitudinally. Shortly before reaching the caudal end, they separate into two divisions, permitting the passage between them of the perpendicular muscle. They curve around this, curve mesad toward each other, and end in a thin fascia that forms a partition between them. When this long muscle contracts, it draws the tooth plate back into the mouth, and then flattens it out again.

But as the long muscle is fixed only at one end, it cannot contract without assistance, hence the perpendicular and circular muscles.

The perpendicular muscle (Müller's "innere senkrechte Muskel der Zunge"), is a short rather stout muscle, arising from a small cartilage on the ventral surface of the "club," and running cephalo-dorsad, where it ends in a bounding fascia (Figs. 3, 4, *p. m.*). This little muscle, surrounded as it is by the long muscle, acts as a fixed point for the latter to contract around, and by contracting itself, increases its diameter as a pillar, and by thus taking up more room, helps the other to contract.

The circular muscle, also one of the mandibular muscles (Fürbringer's *m. copulo-copularis*, Müller's "höherer Aussermuskel der Zunge"), is a hollow cylinder surrounding the long muscle (Figs. 3, 4, *c. m.*). It begins about a quarter of an inch caudad of the tooth plate, and continues to within half an inch of the caudal end of the "club." It is much thicker at its cephalic end, where the long muscle consists of little more than a tendon, than at the caudal end, its walls growing thin there, and the long muscle increasing in girth. It is covered with an aponeurosis into which its fibers are set. Its fibers run circularly at right angles to the long axis of the "club." In cross section the walls of the circular muscle are seen to be crescent-shaped, thick on the ventral surface and at the sides, but thinning as they proceed dorsad, until only a thin layer or fascia is left to

close the cylinder upon its dorsal surface (Fig. 4). The circular muscle by contracting around the long, forces it back to where it has more room in the hind end of the "club," and so helps it to withdraw the tooth plate. Considering the extreme cumbersomeness of this device for using the lower jaw, it is rather remarkable that the hagfish can move it with the lightning-like rapidity with which it does.

If the fish is large enough to permit of it, the hagfish makes only one opening in the skin, and pushing in through that, works its way around inside, eating as it goes. I have seen three hagfish attack one fish through the same opening, their heads entirely hidden in the fish's body, their tails flapping like streamers in a wind as they pushed the fish in front of them, each striving to outdo its neighbor. They usually eat together, and I have often seen several of them at work on one dead fish, while other fish would be lying untouched in the aquarium. Under these circumstances it is no longer permissible to hold that the large fish found to be reduced to skin and bones, have been thus denuded by a single hag, though it may well be that only one of the number is detected in the act of leaving it.

The hagfish do not eat often. After the first feeding in captivity, a week passed before they were given anything more. Then flounders were given again, but only half a dozen ate. A week later, when flounders were offered them for the third time, only three touched them. At the end of another week they were given a rock cod, but did not touch it. Four days after, they were given a small cod and two small flounders, but did not touch them. It was not that the food did not suit them, for they eat any fish on the lines; they were evidently not hungry. Still I thought I would see if a different kind of food would tempt them more, so the next week, thirty-five days after they were caught, and seventeen days since any of them had touched food, and about a month after most of them had fed, I gave them five sardines, very flat fish, about eight inches long and two inches broad. There were about thirty hags in the tank, and by this time most all of them seemed to be hungry, for they ate all but one of the sardines. This was the only time ravenous hunger was observed during the summer. The

moment the first sardine was thrown into the water, the hagfish near it woke up, and went to it ; other fish were thrown in, and in a minute or so the whole tank was alive. They ate ravenously, five or six crowding each other around one sardine. Within a few moments, twenty-one and a half of the two dozen sardines had been disposed of ; the rest they finished during the night. As they seemed to be hungry, six sardines were given them four days later. The first was placed in the water very quietly and with as little jarring as possible ; I had already noticed that an object could be placed quietly in the water without their paying any attention to it. When this first sardine was put in, however, several fish within six or eight inches of it were instantly on the alert, showing that they smelt it. They swam over to it, nosed around it, and ate a little. In a minute or so several fish at a greater distance stirred and came over, and they too nosed around the sardine. Other sardines were then thrown in, but comparatively few of the fish ate, and these only lightly. Although there were more than one hundred hagfish in the tank, only two and a half sardines were disposed of.

They were not fed again for two weeks and a half. Then seven sardines were given them. They woke up instantly and examined them, nosing around them as a dog does around a bone. About a dozen gnawed the fish in various places, and by the next morning three of the sardines were entirely eaten, but the others were untouched.

Of course in making these observations it was impossible to tell which fish fed at the different times, and how long any one fish went without food. But the day after the two dozen sardines were eaten, two fish were taken upstairs and placed in the small aquarium there, where they were kept for a month. During this month a sardine was offered them twice, and left with them for thirty-six hours, but was untouched on both occasions. It is thus apparent that they can go a long time without food, and do not eat nearly so heartily when they do feed as has been supposed. The explanation of the greater hunger of those freshly caught probably lies in the fact that they were rather hungry when they found the food in the trap, and that some of them had not been able to get enough of it to satisfy them.

The question of parasitism can, I think, be answered fully in the negative. There is nothing in their structure to indicate degeneracy, either of the feeding organs, or of the senses with which they search for food. Moreover, they have no means of attaching themselves to living prey, unless that prey is held helpless on a line or in a net. They have neither hooks nor a sucking disc with which to hang on, and the palatine tooth is too short and placed too far back in the mouth to be used for this purpose. They can only swim and bite, and I hardly think they could make much headway with a powerful free-swimming cod or halibut.

There is one food, however, of which the males are extremely fond, and that is the eggs of their own kind. They eat these in great abundance, swallowing them whole. One evening, just before leaving the laboratory, I found a dead fish in the tank. It was a female with eggs almost ready for oviposition, and on lifting it the eggs were pressed out. I left them in the tank, twenty of them all told, to see what would happen. The fish had been fed the day before, and had eaten scantily, so they were not hungry, but by morning all but one of the eggs had been eaten; a day or so later I found the empty shells cast out. The egg is swallowed whole, and its contents slowly digested out of it by osmosis, leaving the shell untouched, or at most with only a prick in it given in passing over the teeth. I have examined several hundred eggs that had been pressed out from the intestine, and were in all stages of digestion, from the first murky clouding to the breaking and drawing off of the contents. In none of them was the shell really broken. In many of the largely digested ones there was no sign even of the pin-hole prick, while in others quite undigested, the perforation of the shell was very evident. It must therefore be purely accidental and in no way necessary to digestion.

SENSE PERCEPTION.

The hagfish has all of the usual sensory nerves and sensory organs, barring the lateral line organs, possessed by the higher fishes, but they are all in a very primitive condition. It was

interesting by experiment to see what use was made of them. The eyes are not exposed on the surface, like those of other fishes, but are covered by the skin, which is, however, translucent for an area of about a square centimeter over them. There is nothing, therefore, to prevent the free passage of light. It has already been stated that when in the tank they would lie sometimes with their heads hidden in the rocks, but just as often with them projecting out into the light. It was suggested to me that this might be due to their wanting open water to breathe, and that possibly, other things being equal, they would prefer the dark. So to test it, two fish were placed in a large pan, three feet long by a foot wide, and half of the pan was covered making it very dark, while the other half was left open. It was a gray day, which made the light in the open end of the pan what they were accustomed to down in the tank. Both the fish were sluggish and did not swim much, but they were disturbed a number of times, and made to change positions. Each time when they settled down they seemed regardless of the light. They would settle quite as often at the light end of the pan as at the dark end. To make a surer test, two lively young fish were placed in a round dish about a foot in diameter and covered with an inch of water. After swimming rapidly for a few minutes, they settled down into tight coils. The dish was placed on the table in the photographic dark room, and a microscope lamp was lighted. The lamp had a light-tight iron chimney, with a curved glass rod coming out opposite the flame to concentrate the light on the disc at its far end. This disc was about a centimeter in diameter. The fish chosen were particularly valuable for the experiment because they were young and the skin over the eyes was unusually clear. In one of them it was transparent, so that I could distinctly see the eye beneath it. In the dark room the circle of light coming from the glass disc was held an inch above the water. It could as well have been at the other end of the room as far as observable results were concerned, for they paid no attention to it. It was moved closer and closer to them, finally being placed under the surface of the water, and within an eighth of an inch of their skin, without obtaining an observable reaction. At all of these differ-

ent distances, the light was moved so as to fall on different parts of each fish's body, eyes, tentacles, head, back, sides, etc., and there was no reaction to it by either hagfish.

In regard to whether they could perceive objects or not, the first thing that I noticed about them was, that when swimming rapidly in crossing the tank from side to side, they would repeatedly strike the tank head foremost; and when one was taken from among the rocks and held for some minutes in the hand or dropped in a corner of the tank, it would proceed very cautiously, moving its head from side to side, keeping its tentacles outstretched, and apparently depending on them for knowledge of its surroundings.

The two young hagfish referred to above I also tested for image perception, holding various objects close over their eyes, and bringing them nearer and nearer. They showed no reaction, no matter how near the object was, until the surface of the body was touched, when they jerked their heads away. These hagfish were neither sleepy nor sluggish, but were undoubtedly normal. The conclusion drawn is, that the perception of variations of light and shade even when extreme, does not irritate the eyes.

The evidence in regard to their hearing is just as negative as that concerning their sight. I was not able to find any noise or sound to which they would respond.

In testing the sense of touch, very different results were obtained. If the tank is jarred, the fish immediately tighten their coils; if they are touched suddenly they jerk their heads away. When they are swimming, and often when they are at rest, the tentacle crown is extended, and the tentacles, moving back and forth, sense the water currents or anything they may strike against. When swimming in search of anything, the tentacles are always on the alert, as tactile outposts or sentinels.

The same two fish that were studied for light perception, were also experimented on for touch and were touched lightly in different places with a straw, a glass rod, and a fine needle. When touched lightly, fish A would not respond, but fish B would jerk itself away. Touching any part of the skin, whether of the head, over the eye, on the back, on the side of the body,

etc., gave the same reaction for each fish ; A, as a rule, reacting less energetically than B. But if the tentacle of either fish was touched, the reaction was much greater, each fish jerking the tentacle sharply aside. There seemed to be no difference in sensitiveness between the base and the tip of the tentacles, and the fish responded the most of all upon being touched in the angle formed by the tentacle with the head. B jerked away when touched directly over the nose, but A did not notice it, and neither gave more attention to being touched over the eyeball than in any other part of the skin.

In most cases when they react to the touch stimulus, they respond by curling the body tighter.

I placed a third young hagfish in the dish with the two, and then tried placing various liquids on or near them by means of a pipette. First as a control, I used ordinary sea water. When a stream of this was directed from a pipette against the tentacles and rim of the nose, they would draw the head a little to one side.

Ordinary alcohol was dropped in the water, one drop after another in front of B, within a half inch of the tip of its nose. Some of the drops touched it in mixing with the water, others did not. The contact of alcohol did not produce observable reaction until after twelve drops had fallen, when it moved away. When fish C was treated the same way, eighteen drops fell before it moved ; the nineteenth touched it and it moved its head aside. B was touched again just as before, and again jerked its head away after the twelfth drop. The thirteenth drop placed in front of it at the usual distance, made it swim off to a different part of the dish. In this new position, eleven drops were given it one by one, and it moved at the eleventh. C, treated a second time, took twenty drops before giving any reaction. The twenty-second made it a little uneasy ; at twenty-three it moved its head slightly, and at twenty-four swam away. I followed it with another drop, and it went back to its old place. Three minutes later, it took five drops that all touched it in mixing. It quivered slightly at the third and fourth, but did not move aside until the fifth.

One drop of hydrochloric acid placed in the water near the fish

will make them jerk violently away if it touches them in any place while mixing with the water. A drop of strong ammonia does the same. The ammonia throws down a precipitate of ammonium chloride on the surface of the water, and if this drifts against them before dissolving they show extreme irritability. In all these cases it is largely the sense of touch that is affected, as the reaction was the same whether the mixing drop touched the tip of the tentacle, the rim of the nose, or the side of the head, and it was the touching of the mixture that produced the effect, except in the case of the alcohol, for it was found that when the visible mixture of the drop of acid or ammonia stopped even an eighth of an inch away from the fish, there was no reaction. With the ammonia this could be seen still more plainly, for wherever the ammonia was dropped, it was not until the ammonium chloride touched the skin, whether on tentacle, tip of nose tube, or skin at the side of the head, that the jerking away occurred. With the alcohol it was sometimes a drop that touched that caused the effect, sometimes not. With the many drops put in, only some of which touched the hag, and those not affecting it, it may be that the sense of smell was excited, or it may be that the alcohol finally irritated the mucous membrane lining the nasal tube, or possibly the skin of the tentacles. The foregoing experiments with the acid and ammonia were begun at half-past three o'clock, and were continued until five. By that time the eels had become very languid and were lying in the crescent shape. The next morning they were all right again.

Notwithstanding the negative results of these experiments in regard to the sense of smell, there is no question but that it is a most serviceable sense for the hagfish. As they cannot see, it is the means by which they know when they are near food. I cannot tell at what distance they can detect an object by the sense of smell. When the dead fish was placed in the tank, as stated above, and the hagfish within six inches were aware of it immediately, it took a perceptible time for those farther off to become so, but the scent reached those as far off as eighteen inches to two feet. How much farther it would go I do not know. It probably varies with different individuals.

I was not able to gather any data as to the sense of taste. So far as may be judged from observable reactions, the senses of touch and smell are the most important in the life of the hagfish. Watching its life for four months and examining its brain, both confirm this. Several times, to see what would happen, I took apart the rockery, transferring it to the other side of the tank. The hagfish, suddenly deprived of their place, were restless. First they moved their heads and the fore part of their bodies, groping around, and then began to swim. They swam in a slow, searching manner, sometimes feeling their way along the side of the tank, and always with their heads moving slowly from side to side, tentacles on the alert. Most of them, when they touched the rocks with a tentacle tip, would recognize them instantly, and go right in. Many on approaching within an inch or an inch and a half of them, would plunge straight for them, probably having smelt them. But there were others that, while searching, would glide directly over the rocks, perhaps even touching them with their bodies or the sides of their heads, or even with their tentacles, yet would give no evidence that they noted their presence; instead, they would continue their search farther afield, and eventually get back to them again.

On the other hand, they sometimes have a wonderful surety of motion. One morning I found one hagfish that had made a loop of its body, and was lying motionless, while three others were swimming through the loop, one after the other. They would dash through, describe a large circle from eighteen inches to two feet in diameter, come back to the starting point, and plunge through again. The hole in the loop was less than two inches across, and in the few minutes that I watched them, not one of the three hesitated, or failed to pass quickly and surely through the loop.

But they do not always carry sense of direction so well. If I took one away from the rocks, and dropped it immediately six or eight inches off, it generally went straight back. But if I held it a minute or so, or dropped it farther away, it would have to search for its resting place. Sometimes it would search and find it; sometimes, not finding it immediately, it would swim slowly around and settle down.

In other ways there is a difference in sensitiveness in the hagfish, showing in the varying strength of the reaction caused by different stimuli. The difference in the two fish with regard to the alcohol was one of these. At one time when two healthy fish were in the small aquarium, I struck the table on which the latter stood with a heavy iron bar, thus giving the aquarium a decided jar. The fish responded by tightening up their coils at the tail end, and then loosening them again, one fish reacting more strongly than the other. I pounded regularly at intervals of about five seconds, and they responded each time, the one always in a slightly more marked degree than the other, but the responses getting less and less, until at the twelfth blow they were no longer given. Half an hour later, when they were lying quietly, I tried again. This time they stopped at the eighth pound. The next day they were apparently more irritable, for they were still responding at the twentieth blow.

Their movements of defence are interesting. When caught, their efforts of escape are purely of the reflex order, trying to slip out of what is holding them. They wriggle and squirm to get away, throwing out their heads and wrapping their tails about one's wrist, but they rarely bite. The tooth plate is a formidable weapon, but they seldom use it as such. Of all the five hundred and fifty hagfish handled last summer, but few snapped, and only one bit. This is in keeping with the experience of others who have handled them.

Their power of reflex action is very strong, and when the head is cut off the body wriggles as violently without the head as it could with it. It will wriggle of itself for several minutes after the head is off, and after it becomes quiet it will respond, if touched, for several hours after the beheading, two or three hours in any case, and with the younger, smaller fish much longer. A fish was stretched out and nailed to a board, and injected through the heart with methylene blue. Forty-five minutes later the head was cut off, and the body thrown into a pan. Two hours after this a second headless body was thrown upon it and the first squirmed and tied itself into a knot.

These reflexes are just as strong in the tail end of the body as in the head end. Once in trying to open a hagfish to remove the

ovary, the fish, although it had already been beheaded, squirmed so that it was almost impossible to operate. The body was cut in half in the hope of quieting it, by cutting through the spinal cord, but both halves squirmed as vigorously as ever.

The most remarkable case of all was that of a young hagfish eleven and a half inches long. It was beheaded before noon. At five in the afternoon its body was opened its entire length. As soon as the instrument touched it, it squirmed vigorously, tying itself into a knot. In ten minutes the examination was over, it was thrown into the ocean, and my attendant at once reported that on touching the water it swam away. It would be interesting to know how long its swimming continued.

In contrast with the spinal cord, the life of the brain cells is short, particularly those in the fore part of the brain. When the fish were beheaded, the brains had to be removed and put into the killing fluid within an hour or they were valueless for histological work.

REPRODUCTION.

The hagfish have only one reproductive organ, a peritoneal fold hanging from the roof of the right half of the body cavity. When the eggs or sperm are ripe, the organ fills the entire right side of the body cavity, but after discharge, it is all absorbed except for a small matrix at the caudal end. In this stage the sex of the organ is distinguishable only by histological examination. It appears as a small thickly gathered frill, the outer edge of which holds a multitude of tiny spheres, the undeveloped ova or sperm spheres respectively. As the hagfish has no external marks of sex, in this stage it requires a microscope to distinguish between male and female animals. As the process of ripening proceeds, the frill becomes thicker, and extends cephalad, the spheres becoming more numerous and the ova growing ovoid in shape. The frill may extend possibly one third of the way cephalad, before its edge becomes thicker, or the sex apparent. I cannot state positively at what length this occurs, but by the time it has grown halfway along the cavity, the edge is at least double in thickness what it was

in the beginning, and the sex plainly marked, the eggs being ovoid bodies, about two millimeters long and the sperm spheres larger than before.

Only between twenty and thirty egg cells develop into mature ova during one cycle, many of those starting development being arrested when from two to six or eight millimeters long, and the other spheres failing to develop. Whether this applies to the sperm spheres could not then be ascertained. No new facts were observed relative to the question of hermaphroditism. This condition was not present in any of the relatively few fish examined by me.

The hagfish oviposits at all seasons of the year, but probably a great many more mature in the spring than at any other season; and I think that no individual deposits eggs more than once a year, perhaps not so often as that. Of those studied by me between July 1 and October 30, about half were in the resting stage where it was impossible to detect sex difference. Among the others I did not find any fully ripe male; of the females only two had reached maturity, and of these but one produced ripe eggs, while the other died from some unknown cause before the eggs were deposited. The eggs are easily felt through the thin body wall in handling the fish, and I had from ten to a dozen fish with very large eggs under observation for six weeks or more, but the time was not sufficient to bring more than the one fish to the point of ovipositing.

The supposition that the greater number of hagfish breed in the spring is also supported by the relative numbers of eggs found at different times of the year. Embryos can be found at any time in various stages of development, but most of those taken even in September are small.

Of thirty-seven embryos gathered between September 8 and September 15, eleven were too small to be taken from the shell, eleven more were less than 30 mm. long, six were between 30 and 40 mm., seven between 40 and 50 mm., one 54 mm., and one 65 mm. This last was evidently within a short time of hatching, as it swam freely when taken from the shell. During this same week only four recently hatched hagfish were brought in, and of these one was 60 mm., one was 80 mm., and one 83

mm. The fourth had lost the fore part of its head so that I could not tell its exact length. I was told by the fisherman that eggs in which blood vessels could be seen were not very numerous before September. Late in September I received several very mature embryos and newly hatched young, and also some eggs in which the embryo was not more than eight millimeters, and was told by the fisherman that if I wished some young about four or five inches long to send for them at Christmas time as they were most easily obtained then.

The eggs are difficult to find. They are almost never taken in deep-water dredging, even in beds where the fish are very numerous. The United States Fish Commission steamer *Albatross* was out for three months in the spring of 1904, exploring the bottom of the Bay of Monterey, and in all that time only one egg was brought up by the dredge. On the other hand, Mr. Frederick Woodworth told me that in dredging for molluscs on a mud bottom at a depth of from twenty to twenty-five fathoms, he had several times brought up hagfish eggs. He says also in answer to a letter of inquiry on the subject: "I find from the fishermen that they have taken strings of eggs in from fifteen to eighteen fathoms with their mesh nets in muddy bottoms; with trawls they have taken them in as deep water as thirty-five fathoms, always on muddy bottoms." The one set of eggs that was laid in my aquarium was laid on the sand bottom, though there were the rock heap and the bare wood for the fish to choose between. Under these circumstances it is certainly probable that the hagfish do not breed in their usual habitat, but seek shallower water and a soft bottom to do so. The explanation for this will be found in the food habits of the young.

In gathering the eggs, aside from dredging, advantage is taken of the fact that they are eaten by the males. The fishermen set traps or lines for the fish, and when they are caught, hold them firmly by the head with one hand and "strip" the body with the other, thus forcing out any eggs or newly hatched young, for these are also eaten. Under these circumstances, only a very small proportion of the eggs obtained are good for histological study, as most of them have been more or less digested. Even if they are sufficiently uninjured to use for his-

tological purposes, the embryo is generally so much hurt that it will not develop further but must be fixed at once.

Hagfish embryos are exceedingly slow in developing. The evidence pieced together from the eggs brought in and the statements made by the fishermen as to the seasons when certain sizes of embryos were most easily found, was confirmed by the development of the seven eggs laid in the aquarium.

The average egg when laid is about twenty-three millimeters long (though some are shorter by several millimeters), and about six millimeters broad at the broadest place. The opercular ring is three millimeters from the animal pole (Fig. 5, *a*). Very rarely a second ring is found at about the same distance from the vegetal pole.

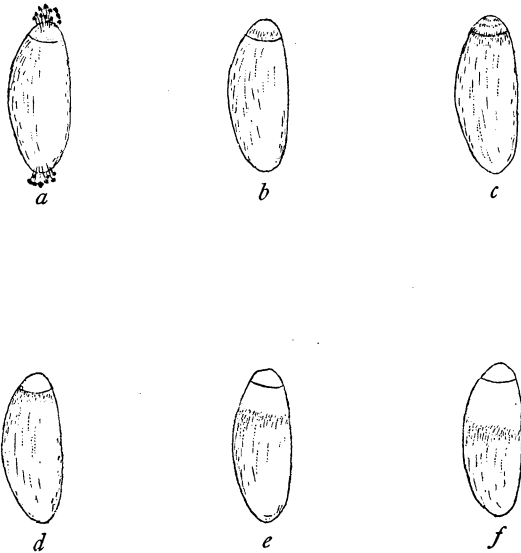


FIG. 5.—Eggs in the early stages of development. *a*, fresh laid egg; *b*, the same egg with the anchor filaments cut off, and showing protoplasmic disc at the animal pole; *c*, three-day egg, showing the terraces; *d*, at the beginning of the fourth day; *e*, the fifth day; *f*, the sixth day. Natural size.

Dean ('99) speaks of the egg being encased, when deposited, in two outer membranes, both of which are shed shortly after laying. Several eggs were brought me by the fisherman that had evidently been secured before they were ripe for oviposition. These eggs were identical with those, mentioned above, that I

had obtained from a hagfish which died in the aquarium. They were covered, anchor filaments and all, with a tough white membrane, translucent, but not transparent. When this was stripped off there was no second membrane inside, but instead, a thick jelly-like substance that filled in all the space between the egg-shell proper and the outer membrane. I do not hold with Dean that this outer membrane and jelly is shed shortly after laying, but think, instead, for two reasons, that the egg is freed from it before being deposited. The set of eggs in this condition taken from the dead fish, was left in the aquarium, and all but one were eaten before morning. That one, however, was left untouched. It had its outer membrane still on it, and remained in this condition. My second reason is, that the eggs normally laid in the aquarium, seven of which had been undisturbed, were, when I first saw them, entirely free from any such structure. They were in two groups, a group of four and a group of three, joined together by their anchor filaments and forming two parallel straight lines. There were no cast off membranes anywhere to be seen, and whatever might have happened to the jelly, the membrane could not have been dissolved by the salt water. Moreover, the eggs were joined by the anchor filaments, which could easily have happened if they were deposited free of membrane and jelly, but would have been impossible otherwise, as there was no force in the tank that could have changed the position of the eggs after they were deposited, or could have arranged them in regular groups. If the membranes were cast off after extrusion, what became of them? If they dissolved (and the one on the egg of the other set was neither dissolved nor cast off), how were the eggs pushed close enough together for their anchor filaments, previously separated by at least two thicknesses of membrane, to interlock?

I transferred the seven recently deposited eggs to a dish, in which was a constant flow of fresh salt water, in the hope that some of them might prove to be fertilized. The fresh eggs were a delicate, brilliant yellow in color with a white mass at the animal pole. I found them Tuesday morning, September 20th. Fig. 5, *a*, shows one in its normal state; *b* is the same egg without the anchor filaments, and shows the protoplasmic mass.

In the evening of the same day, two eggs, *a* and *b*, showed this protoplasmic mass extending halfway between the animal pole and the opercular ring. On the next day *a* had this mass extending two thirds of the way to the ring, while *b* was apparently unchanged. No changes had been noticed in any of the other eggs. Thursday showed no particular change in any of the eggs. On Saturday morning, the fourth day, *a* had a translucent cap, lighter in color than the rest of the egg, extending from the animal pole to one millimeter past the ring (Fig. 5, *d*), while in *b* the protoplasmic mass at the pole came two thirds of the way toward the ring, and was grouped in three distinct terraces (Fig. 5, *c*). The other eggs had merely the protoplasmic mass, coming halfway to the ring.

By three P. M. the same day, the cap of *a* had grown 1 mm. measuring 5 mm. from the pole to its edge at its deepest place. Before noon the next day it had grown 2 mm. more, measuring 7 mm. all told. Egg *b* had lost its terraces, and gained instead a cap, coming to within $\frac{1}{3}$ mm. of the ring, while a third egg, *c*, which had heretofore appeared quiescent, showed a marked terrace. One hour later the cap on *b* had passed the ring by $\frac{1}{3}$ mm. At this time *a* is represented by Fig. 5, *e*; *b* by Fig. 5, *d*; and *c* by Fig. 5, *c*.

Monday, the sixth day, at ten A. M., the cap on *a* was 9 mm. deep, and on *b*, 5 mm.; *c* was still in the terrace state, and terraces were showing faintly on *d*; *a* also had a tiny white dot, 1 to $\frac{1}{2}$ mm. below the ring, and in the middle of the flattened part of the egg. That same day at five P. M. the cap of *a* measured 10 mm. and the white speck was just the same, *b*'s cap was 6 mm. deep, the terraces of *c* and *d* were unchanged, and terraces were beginning to show on *e*; *f* and *g* were as they had been in the beginning. By measuring carefully morning and evening for several days I found that the average rate of growth of the cap after the terrace state was passed, was two millimeters in twenty-four hours, and that the time of highest rapidity was between ten A. M. and five P. M., as much space often being covered then as was covered between five P. M. and ten the next morning.

Tuesday, *a* and *b* were progressing at the usual rate of growth,

c had a cap reaching a little more than a millimeter past the ring, and *f*, in which I had not previously noticed any terraces, had a cap a trifle deeper than that of *c*. The caps in the earlier stages are very hard to detect, as the difference in translucency between them and the rest of the egg is very slight, and the shell somewhat opaque.

Wednesday morning at the end of the first week, *a*'s cap was 13 mm. deep, *b*'s 9 mm., *c*'s 7 mm., *f*'s 8 mm., while *d*, which had shown terraces almost as soon as *c*, lagged behind with a cap of only a little more than $4\frac{1}{2}$ mm.

By five P. M., *a*'s had grown 1 mm., *b* had not changed at all, while on the others the caps had grown 2 mm. each, twice the usual amount. That night, however, they all grew at the regular rate. Meantime, the white speck on *a* was no longer visible. On Friday, the tenth day, in addition to the usual increase in size of the cap, a very fine white line appeared on *c* a little below the ring, whose further history could not be traced.

On Monday, October third, at five P. M., not quite fourteen days after the eggs were laid, the blastopore of *a* was closed. Within a few days the blastopores of the other developing eggs closed also. Within this week, owing perhaps to very hot weather, the eggs died.

But they had lived long enough to confirm the idea of their exceedingly slow growth: fourteen days from the beginning of development to the closure of the blastopore, and no head elevation, or primitive streak showing in this time. In all eggs where the primitive streak shows, or where the young embryo does not extend the full length of the egg, there is a cap over the egg, that extends about one millimeter beyond the tail of the embryo. This second cap, however, is caused by changes in the yolk. With the appearance and growth of the mesoderm, the yolk near the embryo and immediately beneath the shell becomes spongy and full of vacuoles in which lymph and blood spaces are laid out. This gives this part of the yolk a whiter appearance than the rest and so forms a cap.

It is worthy of note that the five eggs that began to develop were supposedly all fertilized at the same time; nevertheless, there was a difference of from one to three days in the starting

of development, and only one started immediately. How shall we account for the uneven rates of growth noticed in one or two eggs afterwards, for instance on the day when *b* did not grow at all, and the others grew twice their usual daytime amount? What caused *f* to lie apparently quiescent for several days, then omit the terrace state, or cut it down to a ten or twelve hours at most, instead of the thirty-six to forty-eight it generally lasts and then growing with a leap, outstrip its brothers *c* and *d*, and finally even *b*? The eggs were all kept under identical conditions, and the most marked variations were in those in the same dish. It would seem impossible for external conditions to affect one without affecting all the others, yet here were decided variations in a process generally much more uniform.

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